Aging of Amateur Singers and Non-singers: From Behavior to Resting-state Connectivity

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Abstract

■ Healthy aging is associated with extensive changes in brain structure and physiology, with impacts on cognition and communication. The "mental exercise hypothesis" proposes that certain lifestyle factors such as singing—perhaps the most universal and accessible music-making activity—can affect cognitive functioning and reduce cognitive decline in aging, but the neuroplastic mechanisms involved remain unclear. To address this question, we examined the association between age and resting-state functional connectivity (RSFC) in 84 healthy singers and nonsingers in five networks (auditory, speech, language, default mode, and dorsal attention) and its relationship to auditory cognitive aging. Participants underwent cognitive testing and fMRI. Our results show that RSFC is not systematically lower with aging and that connectivity patterns vary between singers and nonsingers. Furthermore, our results show that RSFC of the precuneus in the default mode network was associated with auditory cognition. In these regions, lower RSFC was associated with better auditory cognitive performance for both singers and nonsingers. Our results show, for the first time, that basic brain physiology differs in singers and nonsingers and that some of these differences are associated with cognitive performance. ■

INTRODUCTION

The world population is aging. Healthy aging is associated with cognitive, speech, and hearing decline (Tremblay et al., 2018; Tremblay & Deschamps, 2016), with impacts on social activities and social participation, and, more generally, quality of life (Harada, Natelson Love, & Triebel, 2013). In this context, it is important that we learn more about how the brain age. Brain aging can be measured in several ways, including via resting-state fMRI (rs-fMRI), a method that allows for the investigation of brain functions when participants are not engaged in a task (Biswal, Zerrin Yetkin, Haughton, & Hyde, 1995). In a typical rs-fMRI experiment, participants lie on the MRI scanner bed and are asked to think of nothing in particular, without sleeping. They may be asked to close or open their eyes, or to stare at a crosshair fixation mark (Agcaoglu, Wilson, Wang, Stephen, & Calhoun, 2019). rs-fMRI studies focus on measuring the correlation patterns between spontaneous low-frequency (<0.1 Hz) activity emerging from different brain systems (Beckmann, DeLuca, Devlin, & Smith, 2005). The general notion is that regions exhibiting temporally correlated signals are functionally connected. Several resting-state networks have been identified thus far, including the default mode network (DMN) and the dorsal attention network (DAN; Hausman et al., 2020; van den Heuvel & Hulshoff Pol, 2010).

Although aging has been associated with reduced resting-state functional connectivity (RSFC) in multiple networks (Farras-Permanyer et al., 2019; Ferreira & Busatto, 2013; Grady, Grigg, & Ng, 2012; Damoiseaux et al., 2008), especially in the DMN and the DAN (Ferreira & Busatto, 2013), some studies have reported both stronger and lower RSFC associated with normal aging (Farras-Permanyer et al., 2019; Biswal et al., 2010; Jones, Bandettini, & Birn, 2008). A study focusing on visuospatial attention found weaker RSFC between the SMA and the left anterior insular cortex in older adults, which was related to lower visuospatial attention (Li et al., 2015). RSFC decreases have also been documented in neurodegenerative diseases, such as Alzheimer disease (Agosta et al., 2012; Binnewijzend et al., 2012). A recent study showed that the RSFC is lower with age "within" predefined networks and is higher with age "between" networks (Varangis, Habeck, Razlighi, & Stern, 2019). Clearly, the resting networks of the brain evolve with age, but the underlying mechanisms and patterns of changes are not completely understood.

One important question that remains unanswered is the functional impact of age-related changes in RSFC. Understanding not only how the brain changes but also how this affects mental processes and behavior is crucial if we are to develop methods to optimize aging. However, the relationship between RSFC and cognitive performance is not straightforward, as higher connectivity does not necessarily imply better cognitive performance (Ferreira & Busatto, 2013). A study found that participants with stronger RSFC

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had better performance in auditory signaling games (Lumaca, Kleber, Brattico, Vuust, & Baggio, 2019). A recent study showed that higher between-network RSFC is associated to lesser memory, executive function, and language abilities (Zhang, Gertel, Cosgrove, & Diaz, 2021). Similarly, it has been shown that within-network RSFC is higher with age and that higher RSFC is associated with worse motor performance (King et al., 2018). Several models have been developed to account for the impact of brain aging on cognition, including the Compensation-Related Utilization of Neural Circuit Hypothesis (CRUNCH; Reuter-Lorenz & Cappell, 2008) and the Hemispheric Asymmetry Reduction in Older Adults Hypothesis (HAROLD; Cabeza, 2002). Briefly, the CRUNCH model proposes that older adults recruit additional regions to maintain performance even when the task is simple, whereas the HAROLD model proposes that older adults recruit contralateral brain regions during cognitive tasks to maintain performance. None of these models, however, have integrated changes in RSFC to help explain cognitive decline, despite the known relationship between RSFC and cognition (Lumaca et al., 2019; Stevens & Spreng, 2014). As RSFC is an index of baseline brain physiology that is sensitive to brain pathology (Sheffield & Barch, 2016; Skidmore et al., 2013; Sorg et al., 2007), and given that brain pathology can impact cognitive functioning, it appears important to integrate not only task-based fMRI studies but also baseline brain physiology to models of neurocognitive aging.

Although aging is associated with brain senescence and, in turn, cognitive decline, the aging adult brain retains the ability to learn and to transform itself. Learning experiences can modify both the structure and functioning of the brain, a phenomenon known as "experience-dependent brain plasticity." However, the effect of different types of experiences on brain physiology, especially on RSFC, is not fully understood. Musical activities, such as singing and instrument playing, are complex activities that engage the perceptual and motor systems, as well as affective, cognitive, and motivational systems (Miendlarzewska & Trost, 2014). Music performance requires precise timing, fine motor control, auditory perception, and auditory–motor integration (Zatorre, Chen, & Penhune, 2007). Because of this complexity, musical training could have a positive impact beyond the auditory system (Bigand & Tillmann, 2021), potentially affecting speech skills (Patel, 2011), fine motor skills (MacRitchie, Breaden, Milne, & McIntyre, 2020), and inhibitory control (Saarikivi, Putkinen, Tervaniemi, & Huotilainen, 2016), consistent with the mental exercise hypothesis (Salthouse, 2006; Salthouse, Babcock, Skovronek, Mitchell, & Palmon, 1990). A recent meta-analysis from our group shows that musical activities are associated with better speech perception in noise in challenging conditions (Maillard, Joyal, Murray, & Tremblay, 2023). However, the manner in which musical activities affect brain physiology remains largely unknown. It has been shown that the practice of musical activities can affect RSFC. For instance, 24 weeks of piano training for nonmusically trained young adults increased RSFC in the sensorimotor cortex (Li & Li, 2018). Relatedly, Luo et al. (2014) reported significantly stronger RSFC in multiple brain regions in young professional musicians compared with young nonmusicians. Another study has shown stronger RSFC in regions related to autobiographical and semantic memory, as well as in several language-related areas, in professional musicians compared with nonmusicians (Fauvel et al., 2014).

In addition to being associated with RSFC, musical activities are also associated with structural connectivity. For example, a longitudinal study found that children showed a nonsignificant increase in gray matter volume after 1-year instrument training. The children who received training had better performance in other tasks such as fine motor tasks and auditory discrimination skills compared with the control group (Schlaug, Norton, Overy, & Winner, 2005). In another study, the corpus callosum, which connects the left and right auditory processing areas, was found to be larger in adult male musicians (Lee, Chen, & Schlaug, 2003), suggesting that musicians have greater interhemispheric connectivity and auditory information transfer (Westerhausen, Gruner, Specht, & Hugdahl, 2009). Furthermore, radial diffusivity of the transcallosal connectivity between the left and right planum temporal was found to be higher in adult male musicians than male nonmusicians (Elmer, Hanggi, & Jancke, 2016). The microstructural integrity of the posterior third of the corpus callosum was found to be correlated with attentional timing differences in verbal dichotic listening in young adults (Friedrich et al., 2017). In a study from our group, amateur singing was associated with structural differences in the arcuate fasciculus in healthy adults (Perron, Theaud, Descoteaux, & Tremblay, 2021). The arcuate fasciculus connects the temporal cortex and inferior parietal cortex and is considered a major tract for speech and language (Dick, Bernal, & Tremblay, 2014; Dick & Tremblay, 2012). Notably, larger fractional anisotropy in the auditory callosal pathway (genu of the corpus callosum) is associated with better auditory performance in young adults (Lumaca, Baggio, & Vuust, 2021). In summary, musical activities appear to be associated with differences in connectivity, both functional and structural. Given the extensive and well-documented decline in brain structure that occurs with age, including gray (Gozdas et al., 2021; Pistono et al., 2021; Minkova et al., 2017) and white matter atrophy (Gozdas et al., 2021; Perron et al., 2021; Pietrasik, Cribben, Olsen, Huang, & Malykhin, 2020), it is possible that such structural alterations affect the integrity and efficiency of neural pathways, thereby influencing RSFC and cognitive functions (Damoiseaux, 2017; Zhao et al., 2015).

In the present study, we focus on RSFC in singers. Singing is a universal musical activity and one that is accessible and popular at all ages. It requires auditory–motor integration; motor control of the throat, lips, and tongue; constant monitoring of auditory feedback to assess performance; and making rapid and precise sensorimotor adjustments when needed. Similar to playing instruments, singing could have beneficial impacts on brain function and different aspects of behavior, including auditory processing, auditory cognition, speech, and language. However, only a few studies have examined the impact of singing on brain structure (Tremblay & Perron, 2022; Kleber et al., 2016) and function (Tremblay & Perron, 2022; Sihvonen, Pitkäniemi, Leo, Soinila, & Särkämö, 2021; Sihvonen et al., 2020; Dubinsky, Wood, Nespoli, & Russo, 2019; Lumaca et al., 2019; Zamorano, Cifre, Montoya, Riquelme, & Kleber, 2017; Kleber, Veit, Birbaumer, Gruzelier, & Lotze, 2009), and none has examined the relationship between singing and RSFC. In terms of the impact of singing on behavior, it has been shown that 10 weeks of choir singing training can improve speech-in-noise perception, pitch discrimination, and the strength of the neural representation of speech fundamental frequency in older adults (Dubinsky et al., 2019). In another study—the Longitudinal Aging Study Amsterdam—older adults who sang or played a musical instrument performed better with respect to attention, episodic memory, and executive functioning compared with nonmusicians (Mansens, Deeg, & Comijs, 2018). Singing was also reported to be positively associated with faster information processing speed, better inhibitory control, and better auditory frequency discrimination in young and older healthy adults (Tremblay & Perron, 2022). Given what is known about the effect of singing on RSFC and cognition, understanding whether singing has a positive impact on RSFC is important because of the universal accessibility of singing as a potential strategy to promote positive aging.

The general objective of this study was to examine RSFC in healthy young and older amateur singers and nonsingers, focusing on several networks relevant to singing (auditory, speech, language, default mode, and dorsal attention). The specific objectives were (1) to assess the association between age and RSFC in five networks of interest (the auditory network, the speech network, the language network, the DMN, and the DAN), (2) to identify RSFC differences between singers and nonsingers in the same five networks, and (3) to examine the relationship between RSFC and different components of auditory attention as well as auditory discrimination. The main hypothesis was that RSFC would be lower in older adults compared with younger adults in the five networks of interest, but that this pattern would be reduced in singers. Moreover, we hypothesized that stronger RSFC would be linked to better auditory attention.

METHODS

Participants

A nonprobabilistic sample of 85 native speakers of Quebec French aged 20–87 years (mean = 54.11 ± 19.47 years, 50 women) with no history of hearing, speech, language, psychological, neurological, or neurodegenerative disorder was recruited through e-mails, Facebook messages, and posters distributed in the community and at Université Laval, as well as through e-mails and Facebook messages targeting choirs in the Quebec City area. Eligibility criteria were verified through screening telephone interviews. The study was approved by the Comité d'éthique de la recherche sectoriel en neurosciences et santé mentale, Institut Universitaire en Santé Mentale de Québec (#192-2017). All participants provided informed consent.

One participant was excluded because he played a musical instrument regularly in addition to singing. The remaining 84 participants were divided into two groups: 43 nonsingers and 41 amateur choral singers. The sample size was based on previous studies with similar or smaller sample sizes that examined age and/or music-related effects on RSFC. Specifically, recent fMRI studies with 84 and 41 participants have found robust age effects on RSFC (Grady, Sarraf, Saverino, & Campbell, 2016; Li et al., 2015). Furthermore, studies with 31–56 participants have found group differences in RSFC while comparing musicians and nonmusicians (Li & Li, 2018; Amad et al., 2017; Luo et al., 2014). Hence, the current sample of 84 was deemed appropriate to address our objectives.

Amateur singers were defined as individuals singing in a choir for at least 2 years with a minimal weekly practice of 60 min. Nonsingers were defined as individuals who do not participate in any form of amateur or professional singing. All participants were right-handed according to the Edinburgh Handedness Inventory (score ≥ 60%; Oldfield, 1971). The general cognitive functioning of the participants was evaluated using the Montreal Cognitive Assessment Scale (Nasreddine et al., 2005); hearing was measured as pure-tone thresholds in dB HL with a calibrated clinical audiometer (AC40, Interacoustic). Participants' characteristics are detailed in Table 1. As seen in the table, nonsingers and singers did not differ in age, sex, education, handedness, and cognition (all ps > .05). For each participant, we calculated a brain health score based on the medication that participants reported taking. We focused on hypertension, hypercholesterolemia, and type 2 diabetes because of their documented relationship with brain disease (Silva et al., 2019). Participants with a score of 0 presented with no such condition, whereas those with a score of 3 presented with all three conditions. The groups did not differ in brain health ($p = .72$).

All participants answered a questionnaire on their musical experiences. The choral singers had an average of 17.68 ± 14.14 years of continuous choral singing experience (range: 2–62 years). All singers sang in a choir once a week for a minimum of 1 hr. Besides singing in a choir, 16 singers (39%) practiced at home every day, 17 (41%) practiced at least once a week, 1 (2%) practiced at least once a month, and 2 (5%) practiced less than once a month; five singers (12%) did not practice outside their weekly choir. Finally, most singers (30 of 41, 73%) had never received formal singing training. Among the nonsingers, 11 (26%) had previous experience with group singing. Six of them stopped singing 30–60 years before the experiment, three of them stopped singing 7–15 years before the experiment, and one of them

Table 1. Participants Summary

Feature	Nonsingers (n = 43, 22 F) *M*	*SD*	*Min*	*Max*	Singers (n = 41, 27 F) *M*	*SD*	*Min*	*Max*	t Test *t*	*p*
Age	54.0	19.5	20.0	86.0	55.0	19.3	22.0	87.0	−0.2	.83
Education[a]	17.0	2.7	12.0	25.0	16.2	3.4	7.0	25.0	1.3	.85
Handedness[b]	93.6	10.0	60.0	100.0	95.8	8.6	66.7	100.0	−1.1	.28
MoCA (/30)[c]	27.5	2.2	21.0	30.0	27.5	1.9	23.0	30.0	0.1	.96
Health (/7)[d]	5.2	0.9	3.0	7.0	5.1	1.0	3.0	7.0	0.3	.75
Right ear PTA[e]	14.8	11.9	−5.0	56.7	11.0	7.9	0.0	33.3	1.7	.09
Left ear PTA[e]	12.4	8.9	−3.3	31.7	7.9	7.2	−3.3	25.0	**2.5**	**.01**
Better ear PTA[e]	10.7	9.0	−5	31.7	7.4	6.9	−3.3	25	1.9	.06
Brain health score (/3)[f]	0.6	0.9	0.0	3.0	0.5	0.8	0.0	3.0	0.4	.72

[a] Number of years of education based on the highest degree obtained in Quebec.

[b] The handedness was measured with the Edinburgh Handedness Inventory. A lateralization quotient of 60% or more indicates laterality on the right.

[c] Montreal Cognitive Assessment. Higher scores indicate better cognitive functions. A cutoff of 20/30 has been proposed to avoid false positive (Waldron-Perrine & Axelrod, 2012).

[d] Self-reported general health status on a scale of 0–7 (0 being the lowest health level).

[e] Pure-tone average (PTA) thresholds measured in decibels at 0.5, 1, and 2 kHz for each ear.

[f] This compound score was computed by summing the presence of each of the following illnesses: hypertension, hypercholesterolemia, and type 2 diabetes. A score of 0 indicates no illness, whereas a score of 3 indicates the presence of all three.

stopped singing 1 year before our study after only 3 months of singing experience. The others had 5 months to 12 years of singing experience (mean = 4.00 ± 3.58 years). Those with the most years of experience stopped singing decades before our study.

Procedures

The experiment included two visits on two separate days. The first visit took place in a double-walled sound-attenuated room at the Speech and Hearing Neuroscience Laboratory in Quebec City, Canada. It included audiometric evaluation and the Test of Attention in Listening (TAiL; Zhang, Barry, Moore, & Amitay, 2012). The second visit involved a multisequence MRI data acquisition session and took place at the Clinic IRM Québec-Mailloux in Québec City. The data detailed here represent a subset of a larger project. Other components of the project have been published elsewhere: a speech perception in noise task and structural imaging data (T1w and diffusion MRI data; Perron, Vaillancourt, & Tremblay, 2022; Perron et al., 2021) and a standardized passage reading task (Marczyk, Belley et al., 2022; Marczyk, O'Brien, Tremblay, Woisard, & Ghio, 2022). A detailed investigation of the cognitive assessments was previously published (Tremblay & Perron, 2022).

For the cognitive evaluations, participants were seated facing a 24-in. computer monitor and were wearing headphones (DT 770 Pro, Beyerdynamic, Inc.). All tests were run on a Lenovo ThinkPad W510 computer. The volume was adjusted to a comfortable level before each task to ensure that performance was not affected by hearing.

Auditory Cognitive Evaluation

All participants completed a cognitive evaluation that included a French version of the TAiL (Zhang et al., 2012), a listening attention test based on Posner's attention system theory (Petersen & Posner, 2012; Posner & Petersen, 1990) and on the load theory of attention (Murphy, Groeger, & Greene, 2016; Lavie, 1995; Lavie & Tsal, 1994). The detailed results of the cognitive assessment have been published elsewhere (Tremblay & Perron, 2022).

The TAiL measures auditory information processing speed and two aspects of auditory selective attention: involuntary orienting (IO) and conflict resolution (CR). The test consists of asking participants to listen to sequentially presented pairs of pure tones presented through circumaural headphones. The test includes three tasks: a cued RT task, an attend frequency (AF) task, and an attend location (AL) task. In the cued RT task, participants were

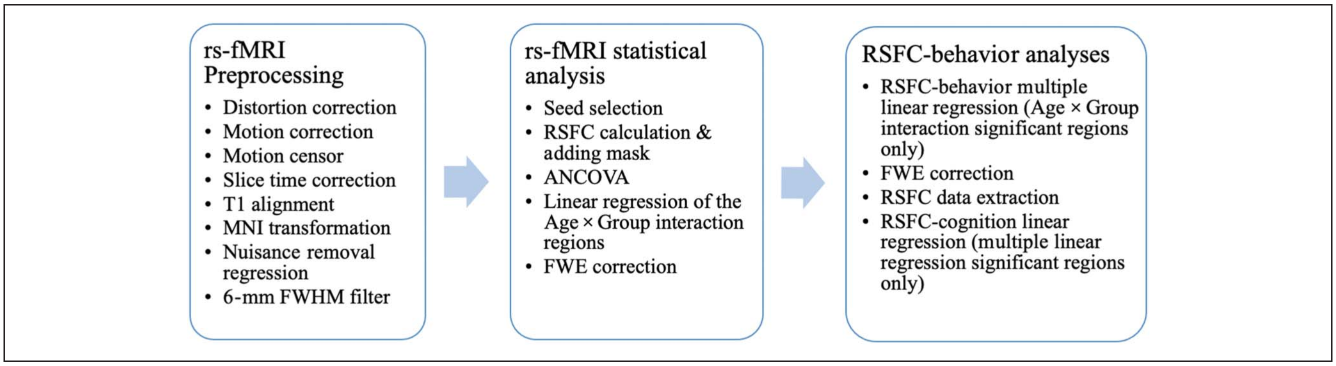


Figure 1. Summary of the data processing steps.

asked to press a key as fast as they can once they heard the second sound. The average RT was recorded to measure the detection of the signal and the speed of auditory information processing. Trials with RTs shorter than 100 msec or longer than 2 sec were excluded. In the AF task, participants were asked to indicate whether the pure tones have the same pitch (which varied between 476 and 6178 Hz). In the AL task, participants were asked to indicate whether the two sounds came from the same ear. In the AF and AL tasks, participant's attention was oriented to the task-relevant dimension (frequency in the AF task, location in the AL task). However, participants could still be distracted by the unattended dimension (location in the AF task, frequency in the AL task). The RT and error rate (ER) are usually higher in situations where the two dimensions are conflicting (i.e., when stimuli are the same in one dimension [e.g., same pitch] but not the other [e.g., different ears]) compared with when they are congruent (i.e., when both the frequency and location are the same or when both are different). It is expected that processing information is more costly in terms of RT and accuracy in incongruent situations. The average RT and the ER were calculated for each task and used to calculate the main outcome measures: an IO score and a CR score (Zhang et al., 2012). The IO score measures the effect of incongruence in the unattended dimension on performance. A higher score indicates higher distractibility. The CR score measures the difference in performance between incongruent and congruent trials. A higher score indicates higher costs for resolving conflict. In a previous study, we found that cued RT, IO score based on ER (IOER), IO score based on RT (IORT),

Table 2. RSFC Cluster Results in the Five Networks

				Peak Values				
Network	*Effect*	*Description of the Cluster*	*Voxels*	*x*	*y*	*z*	*t*	*p*
A. Auditory network	Age	Left insula, left postcentral gyrus	162	−36	−22	5	3.95	<.001
B. Speech network	Age	Left TTG, left STG, left IFG opercular part, left MTG, left planum temporale	265	−65	−24	−1	3.95	<.001
		Right TTG, right STG, right IFG opercular part, right MTG, right planum temporale	201	69	−24	−8	3.82	<.001
		Bilateral SFG, bilateral CG	86	5	−13	50	3.01	.004
C. Language network	Age	Left IFG	79	−53	37	16	−5.44	<.001
		Left IFG, left orbitofrontal gyrus	49	−46	24	3	3.23	<.001
D. DMN	Age	Bilateral SFG, bilateral CG, bilateral MFG	694	5	50	42	−6.66	<.001
	Age × Group interaction	Bilateral superior parietal lobule, bilateral CG, bilateral precuneus	210	−14	−50	29	−3.19	.002
E. DAN	Age	Bilateral SFG, bilateral CG, bilateral superior rostral gyrus	560	2	65	−10	−4.42	<.001
		Bilateral striate area, bilateral precuneus	211	−1	−54	12	−4.17	<.001
		Left orbital gyrus	87	−17	43	−16	4.66	<.001

The clusters were corrected using FWE.

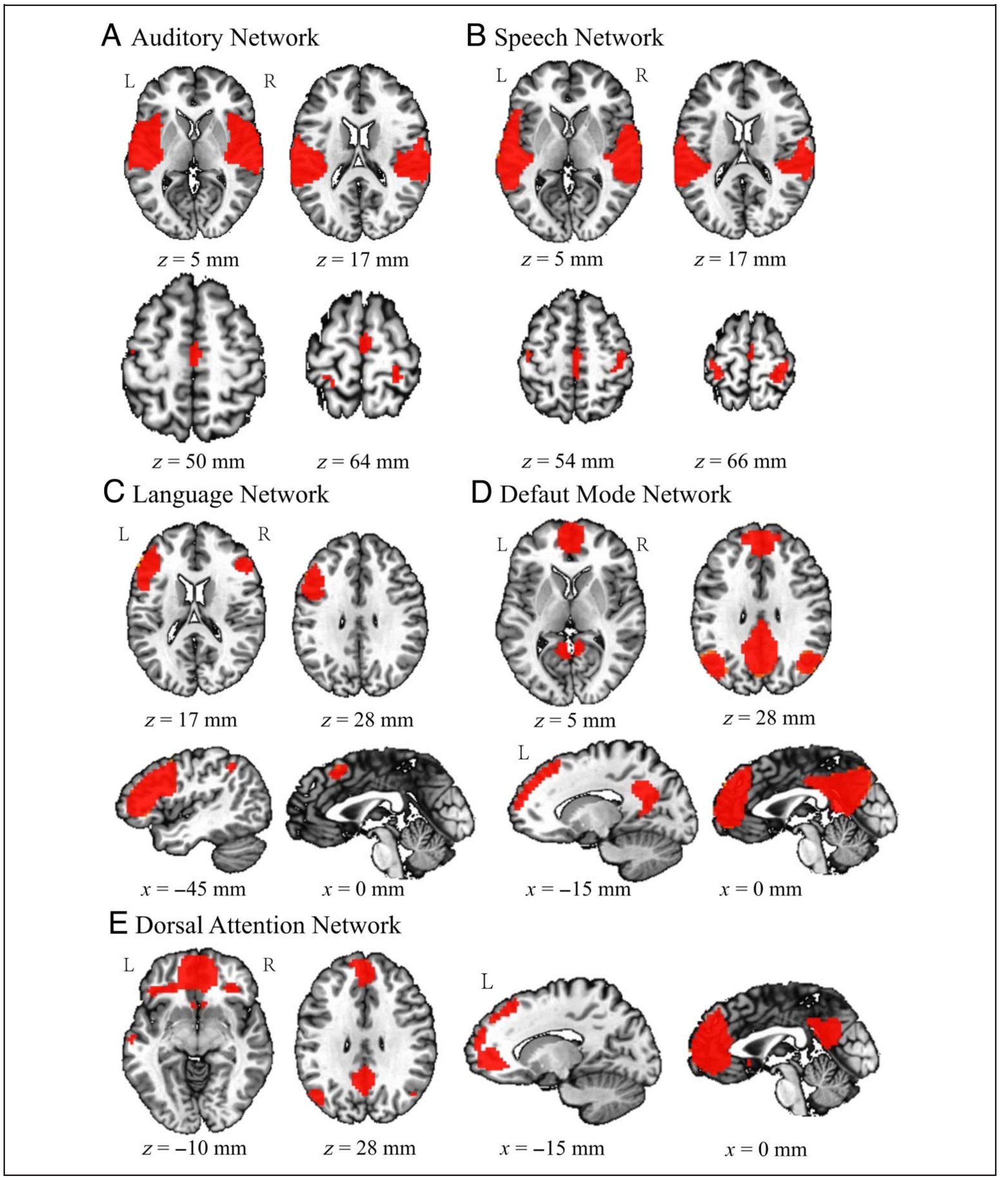


Figure 2. Illustration of the five networks. L = left hemisphere; R = right hemisphere. (A) The auditory network (voxels correlation with the auditory seed, $r \geq .35$) displayed on axial and sagittal slides of the MNI TT_N27.nii average brain (Holmes et al., 1998). (B) The speech network. (C) The language network. (D) The DMN. (E) The DAN.

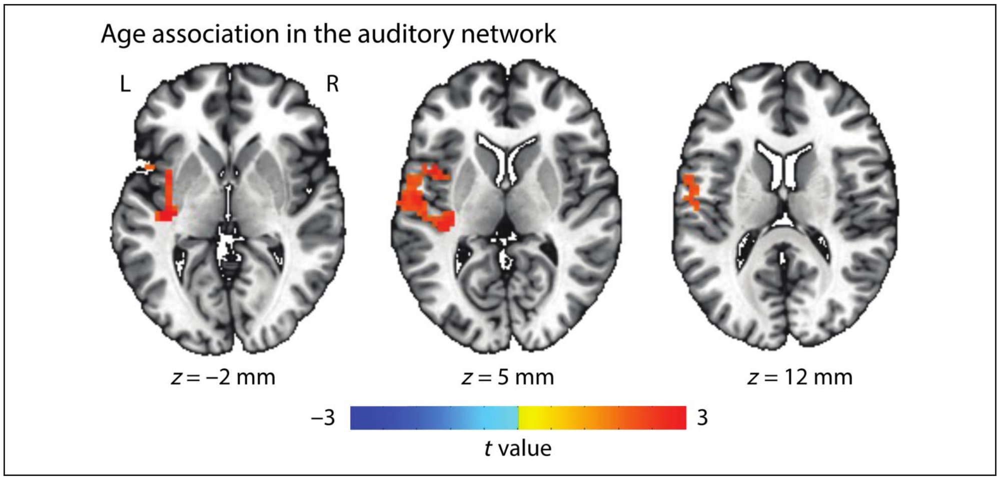
and CR score based on ER (CRER) showed either a group or an age by group interaction. The CR score based on RT was not affected by group (Tremblay & Perron, 2022). In the present study, we decided to investigate the relationship between RSFC and the scores that showed a group effect or an interaction between age and groups in our previous study (cued RT, IOER, IORT, and CRER).

In addition to these scores, we also calculated an auditory sensitivity (d') score to measure auditory frequency discrimination (as a proxy for musical skills; Tremblay & Perron, 2022) with the equation: z (hit rate) minus z (false alarm rate), where hit rate is the proportion of identical trials to which participants responded "identical" and false alarm rate is the proportion of identical trials to which participants responded "different" (Macmillan & Creelman, 1991). A high value of d' indicates a good auditory frequency discrimination capacity. Given that this metric exhibited a strong group difference in our previous study (singers > nonsingers), it was also included in the present study.

MRI Data Acquisition

The data were acquired on a whole-body Philips 3.0 Tesla Achieva TX. The head of each participant was immobilized with a set of cushions and pads during the procedure. The participants were asked to keep their eyes open to avoid falling asleep during the scan. Structural MR images were acquired with 3D T1-weighted MPRAGE sequence (repetition time = 8.4 msec, echo time = 4 msec, field of view = 240 mm, flip angle = 8°, 240 × 240 matrix, 180 slices/volume, slice thickness = 1 mm, no gap, SENSE = P reduction (AP) = 1, S reduction (RL) = 2). Resting-state fMRI data were acquired using 200 single-shot EPI images with the following parameters: repetition time/echo time = 2500/30 msec, field of view = 240 × 240 mm, 80 × 80 matrix, flip angle: 90, 45

Figure 3. Relationship between age and RSFC in the auditory network displayed on axial slices of the MNI TT_N27.nii template ($p < .05$, FWE corrected cluster size > 33).



interleaved 3 mm^3 axial slices, no gap, SENSE = 2.09. Each functional EPI run began with five dummy scans to allow the magnetization to stabilize to a steady state. Two additional diffusion weighted spin-echo EPI images were acquired for distortion correction. The distortion is caused by the susceptibility distribution of the head and rapid switching of eddy currents. The two additional acquisitions with opposing polarities of the phase-encode blips (A-P, P-A) sample opposite distortions within the same field. The two images were used to estimate and correct the distortion.

fMRI Data Preprocessing

The resting-state fMRI data were preprocessed using AFNI V 22.0.04 and FSL V.6.0.5. First, susceptibility-induced distortion was corrected using FSL Topup algorithm using a method similar to that described in Andersson, Skare, and Ashburner (2003) as implemented in FSL (Smith et al., 2004). Next, the data were processed using afni_ proc.py (Jo et al., 2013), which includes motion correction, motion sensor, slice-time correction, T1 alignment, nonlinear Montreal Neurological Institute (MNI) transformation (using the TT_N27.nii template) and nuisance removal regression. The time series were then smoothed using a 6-mm FWHM filter. The results of each step were verified by both authors.

fMRI Data Analyses

Five seeds were selected: one for the auditory network, the speech network, the language network, the DMN, and the DAN based on meta-analyses on neurosynth.org. The auditory seed was located in the left transverse temporal gyrus (TTG; MNI coordinates: −50 −18 6). The speech seed was in the left superior temporal gyrus (STG; MNI coordinates: −60, −20, 2). The language seed was in the left inferior frontal gyrus (IFG), triangular part (MNI coordinates:

Figure 4. Relationship between age and RSFC in the speech network displayed on coronal slices of the MNI TT_N27.nii template ($p < .05$, FWE corrected cluster size > 48).

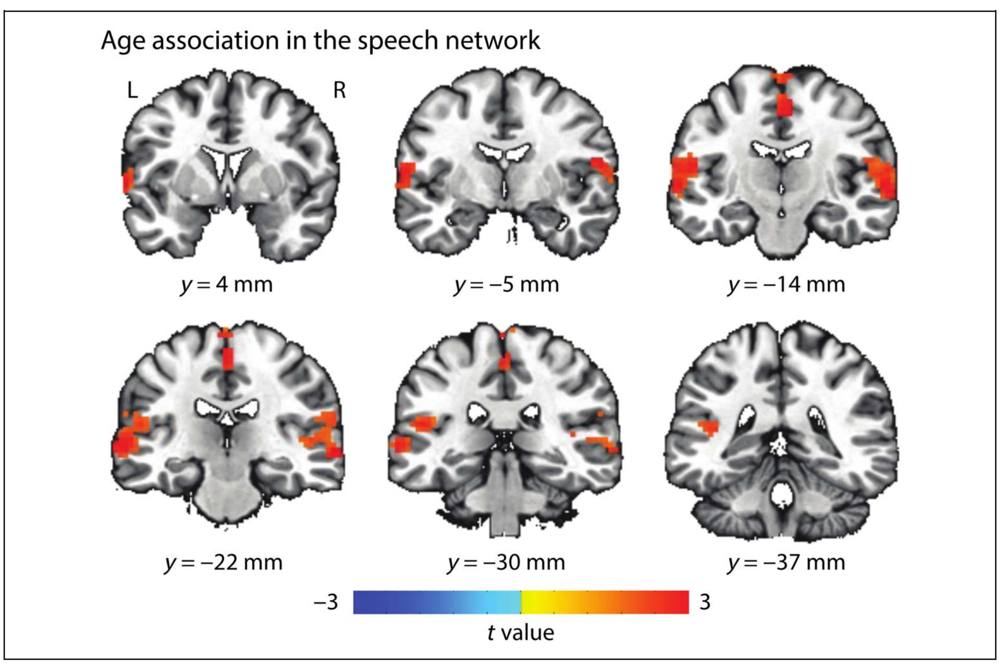
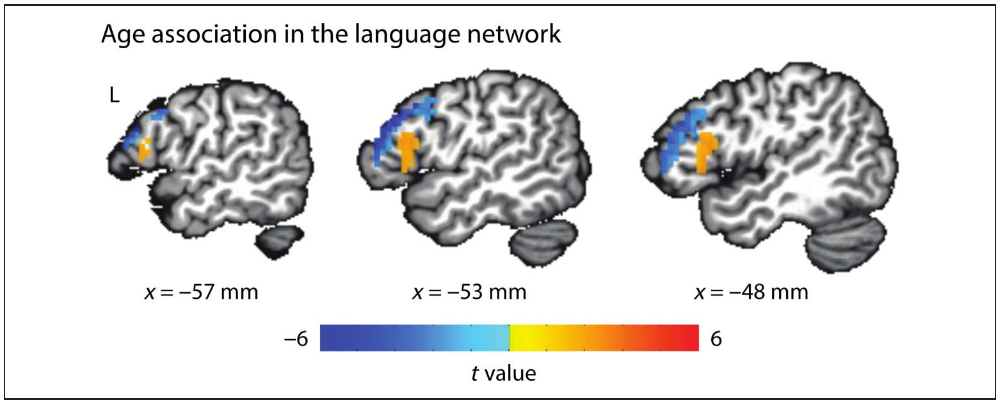


Figure 5. Relationship between age and RSFC in the language network displayed on sagittal slices of the MNI TT_N27.nii template (p < .05, FWE corrected cluster size > 30).

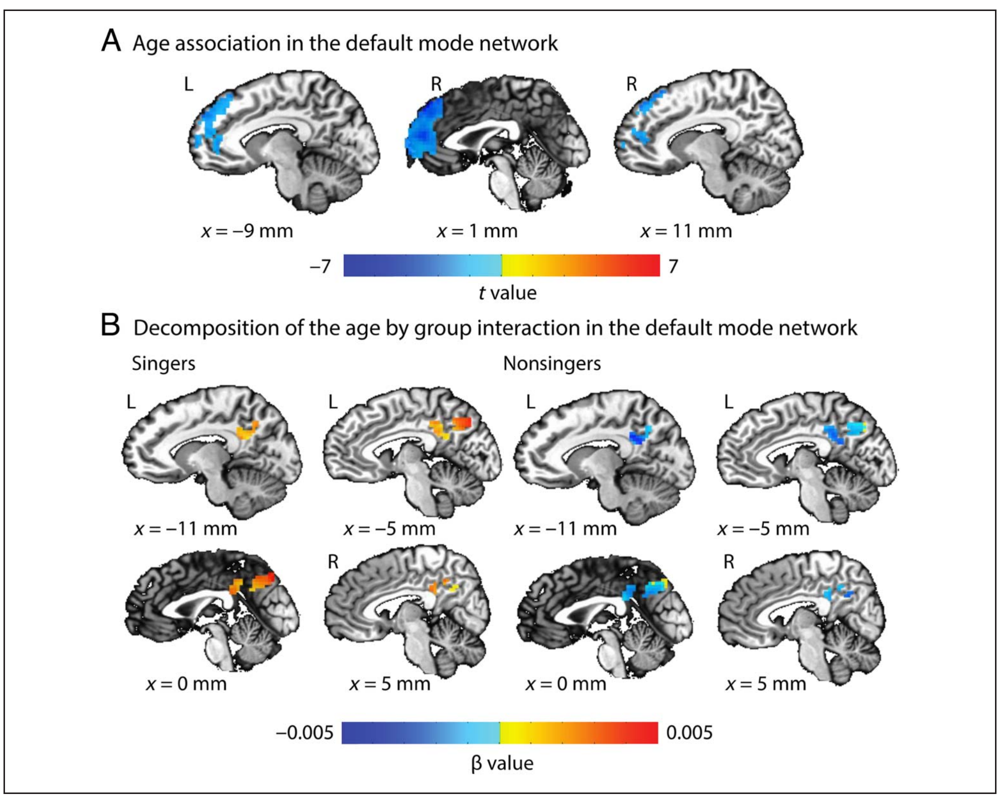


−50 30 16). The DMN seed was located in the left posterior cingulate gyrus (CG; MNI coordinates: −2 −52 26). The DAN seed was in the left angular gyrus (MNI coordinates: −54 −52 46). AFNI *3dUndump* was used to extract the seed masks with a radius of 6 mm. The time series were extracted for each participant using 3dmaskave.

Next, functional connectivity maps were created using 3dTcorr1D. First, we created a group mask for each network by calculating the correlation of all the voxels and the seed. Only voxels with a Pearson's r correlation of ≥.35 were included in the mask to avoid spurious correlations (see mask details in Figure 2). The Pearson's correlations were normalization to z scores via Fisher's r-to-z transformation. A series of ANCOVAs were conducted separately for each of the five networks using *3dMVM* (Chen, Adleman, Saad, Leibenluft, & Cox, 2014). Between-subject factors were Group and Age; sex and brain health score were included as covariates. Because sex and brain health score did not affect RSFC, the final model only included age and group. The RSFC results were corrected using familywise error (FWE) rate using AFNI *3dClustSim*, with alpha = .05, p value = .01, NN = 1, bi-sided. To further decompose the interaction effect, for each network, RSFC was masked with regions that exhibited a significant Age × Group interaction. RSFC in these regions was linearly regressed using AFNI *3dRegAna*, separately for the singers and nonsingers, to assess the effect of age on RSFC in each group.

To address Objectives 2 and 3, that is, to identify potential differences in the aging of RSFC between singers and nonsingers in the five networks of interest and their relationship to cognitive performance, the areas that showed significant Age × Group interaction were further analyzed.

Figure 6. (A) Relationship between age and RSFC in the DMN displayed on sagittal slices of the MNI TT_N27.nii template (p < .05, FWE corrected cluster size > 172). (B) Decomposition of the interaction between age and group in the DMN. The regression between age and RSFC is shown separately for singers and nonsingers (p < .05, FWE corrected cluster size > 172, sagittal view). Red indicates a positive association with age, whereas blue indicates a negative association between RSFC and age. Only regions identified through the ANCOVA analysis are shown.



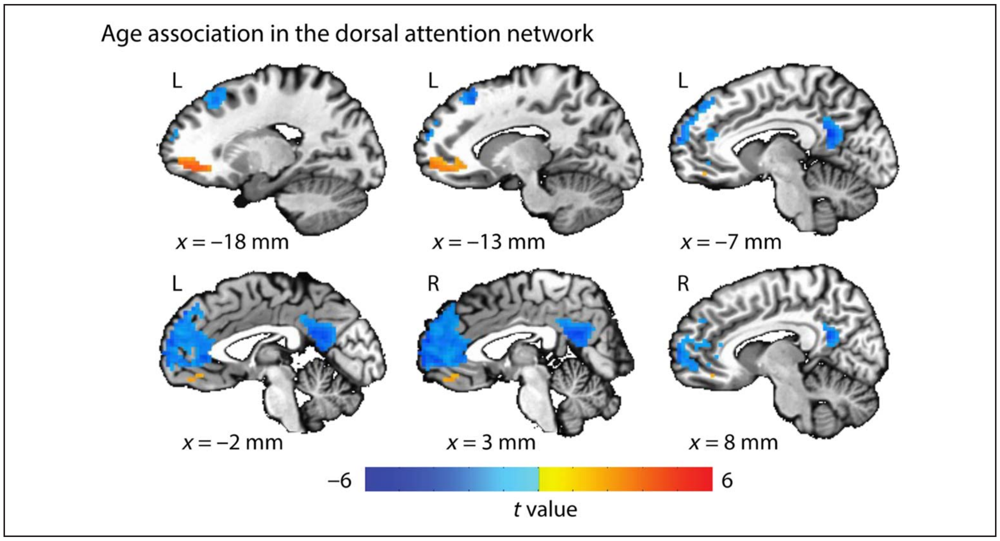


Figure 7. Relationship between age and RSFC in the DAN displayed on sagittal slices of the MNI TT_N27.nii template ($p < .05$, FWE corrected cluster size > v53).

Using multiple linear regressions (*3dRegAna*, AFNI), RSFC in these regions was regressed with age, sensitivity (d') score, cued RT, IOER, IORT, and CRER, separately for each group. The interaction of Age and each behavioral variable was also included in the model. The regression formula is shown below. The resulting maps were corrected using FWE (alpha = .05, p value = .01, NN = 1, bi-sided).

$$\text{RSFC} \sim \text{Age} + d' + \text{Cued RT} + \text{IOER} + \text{IORT} + \text{CRER} + \text{Age} \times d' + \text{Age} \times \text{Cued RT} + \text{Age} \times \text{IOER} + \text{Age} \times \text{IORT} + \text{Age} \times \text{CRER}$$

Next, the mean RSFC of the clusters significantly associated with behavioral variables were calculated for each participant to examine the relationship between RSFC, age, and cognition using R (Version 4.2.2). The processing steps are summarized in Figure 1.

RESULTS

In this section, we present the results of the main analysis for each network separately (Age and Group Effects on RSFC section). The detailed results are provided in Table 2. Next, we present the brain–behavior analysis (RSFC and Auditory Cognition section). The auditory network, speech network, language network, DMN, and DAN masks are shown in Figure 2.

Age and Group Effects on RSFC

The Auditory Network

In the auditory network, RSFC was positively associated with age in the left insula and the left postcentral gyrus (Figure 3). There were no Group differences and no Age × Group interaction. The detailed results are presented in Table 2A.

The Speech Network

In the speech network, RSFC was positively associated with Age in the bilateral TTG, bilateral STG, bilateral IFG opercular part, bilateral middle temporal gyrus (MTG), bilateral planum temporale, bilateral superior frontal gyrus (SFG), and bilateral CG, as shown in Figure 4. There were no Group differences and no Age × Group interaction. The detailed results are presented in Table 2B.

Table 3. Behavior Cluster Results

					Peak Values				
Networks	*Groups*	*Behavioral Measurements*	*Description of the Cluster*	*Voxels*	*x*	*y*	*z*	*t*	*p*
DMN	Singers	Age × IORT	Bilateral precuneus	12	−1	−71	44	2.96	.005
		Age × CRER	Bilateral precuneus	7	−1	−68	47	2.57	.015
	Nonsingers	IORT	Bilateral precuneus	13	2	−68	44	−2.76	.009
		Age × IORT	Bilateral precuneus	9	−1	−68	47	2.50	.017

The clusters were corrected using FWE.

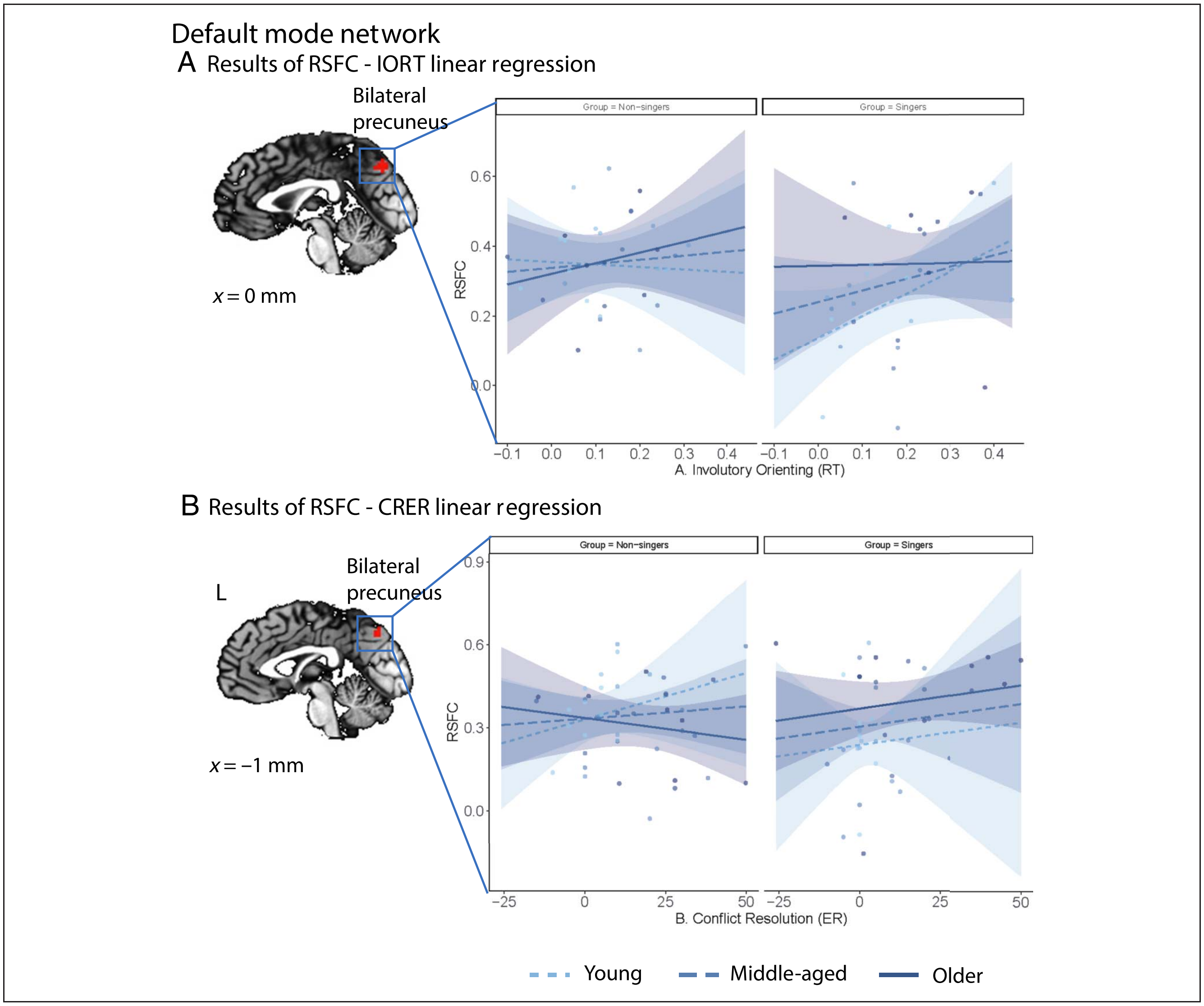


Figure 8. Results of the brain–behavior analysis and the linear regression results of the mean RSFC of the significant Clusters A and B in the DMN. Red indicates the regions significantly associated with cognition variables. (A) Regression results of the regions associated with IORT. (B) Regression results of the regions associated with CRER. IORT = IO score based on RT; CRER = CR score based on ER . Lower IORT or CRER cost scores indicates better performance in the TAiL.

The Language Network

In the language network, RSFC was positively associated with Age in the left IFG and negatively associated with Age in the left IFG and the orbitofrontal gyrus (Figure 5). There were no Group differences and no Age × Group interaction. The detailed results are listed in Table 2C.

The DMN

In the DMN, RSFC was negatively associated with Age in the bilateral SFG, bilateral CG, bilateral middle frontal gyrus (MFG; shown in Figure 6A). There were no Group differences. However, RSFC in the bilateral superior parietal lobule, bilateral CG, and bilateral precuneus showed an Age × Group interaction effect. Linear regressions were conducted separately for the singers and nonsingers to decompose these interactions. As shown in Figure 6B, RSFC was positively associated with Age in these regions in singers. In nonsingers, RSFC was negatively associated with Age in these regions. The detailed results are listed in Table 2D.

The DAN

In the DAN, RSFC was negatively associated with Age in several regions including the bilateral SFG, bilateral CG, and bilateral superior rostral gyrus. RSFC was positively associated with Age in regions including the left orbital gyrus. The regions are shown in Figure 7. The detailed results are presented in Table 2E. There were no Group differences and no Age × Group interaction.

Table 4. Estimates (*b*) of the Relationships Presented in Figure 8

			Nonsingers						*Singers*					
			Young		*Middle-aged*		*Older*		*Young*		*Middle-aged*		*Older*	
Network	*Behavioral Measurements*	*Description of the Cluster*	*b*	*p*	*b*	*p*	*b*	*p*	*b*	*p*	*b*	*p*	*b*	*p*
DMN	IORT	Bilateral precuneus	−0.072	.861	0.116	.687	0.304	.466	0.636	.079	0.331	.216	0.026	.948
	CRER	Bilateral precuneus	0.003	.365	0.001	.665	−0.002	.493	0.002	.780	0.002	.634	0.002	.388

b = unstandardized estimate of the slope; IORT = IO score based on RT; CRER = CR score based on ER.

RSFC and Auditory Cognition

To address our third objective, namely, to examine the relationship between RSFC and auditory cognition, we examined the relationship between RSFC and auditory attention within the networks that showed Age × Group interactions (i.e., the DMN). RSFC in regions showing an interaction was first averaged within participants and then extracted. Next, linear regressions were used to test for a relationship between RSFC and auditory attention (IOER, IORT, CRRT, and CRER) and auditory frequency discrimination (d'). The detailed results are presented in Table 3.

In the DMN, RSFC in the bilateral precuneus significantly showed an Age × IORT interaction (Table 3). The mean RSFC of each participant was regressed using the following formula: RSFC ~ Age × Group × IORT. Figure 8A reveals that RSFC in the bilateral precuneus was negatively associated with IORT in both nonsingers and singers. Specifically, in the nonsingers, higher RSFC was associated with worse IORT for older and middle-aged participants, but not for young adults. In singers, age did not moderate the relationship between RSFC and IORT in older participants. For the middle-aged and young adults, higher RSFC was associated to worse IORT.

RSFC in the bilateral precuneus was significantly associated with CRER and showed an Age × CRER interaction (Table 3B). The mean RSFC of each participant was regressed using the following formula: RSFC ~ Age × Group × CRER. As shown in Figure 8B, lower RSFC was associated to lower distractibility in young and middle-aged nonsingers and singers. Higher RSFC was associated to lower distractibility for the older nonsingers. Higher RSFC was associated to higher distractibility for middle-aged and older nonsingers. The p values of the slopes of the simple regression analysis are presented in Table 4.

DISCUSSION

We designed this study to examine brain aging in healthy young and older amateur singers and nonsingers using RSFC as an index of brain functioning and brain health. We focused on five networks relevant to singing: the auditory network, the speech network, the language network, the DMN, and the DAN. To our knowledge, this study is the first to investigate experience-induced plasticity in RSFC in amateur singers and nonsingers. To understand potential differences between the groups and their impact on functioning, we examined the relationship between RSFC and different components of auditory attention. Given the importance of attention on daily activities and global functioning and the well-established decline in attention and, more generally, executive function that occurs in aging (Harada et al., 2013), finding new ways to promote healthy aging should be a priority. In the subsequent paragraphs, first, we review and interpret the age effects that were found within relevant theoretical frameworks, and next, we address singing-related results.

Age Effects

The first specific objective of this study was to assess the association between age and RSFC in five networks of interest. Our main hypothesis was that RSFC would be lower in older adults. Our results support this hypothesis in the language network (left orbital IFG), the DMN (bilateral SFG, bilateral CG, bilateral superior rostral gyrus), and the DAN (bilateral SFG, bilateral CG, bilateral superior rostral gyrus, bilateral striate area, bilateral precuneus). These findings are largely consistent with the literature. In a large-scale fMRI study, task-based functional connectivity was lower with age in the DMN and the DAN (Andrews-Hanna et al., 2007). A lower RSFC in the DMN with age has been reported in several studies (Onoda, Ishihara, & Yamaguchi, 2012; Wu et al., 2011; Koch et al., 2010; Wang et al., 2010). In the DAN, lower RSFC has been reported in healthy older adults compared with younger adults (Tomasi & Volkow, 2012).

However, our results in some regions do not support the hypothesis of a negative association between age and RSFC, such as in the left insula and left postcentral gyrus (auditory network), left TTG, left STG, left opercular part of IFG, left planum temporale (speech network), left IFG and left orbital frontal gyrus (language network), and the left orbital gyrus (DAN). In these regions, RSFC was higher in older compared with younger adults. Higher RSFC in older adults has been reported in the literature. Some studies investigated predefined resting-state networks have reported higher RSFC with age "between" (but not within) networks (Zhang et al., 2021; Varangis et al., 2019; Chan, Park, Savalia, Petersen, & Wig, 2014). This could reflect a compensatory mechanism, where the brain adapts to structural or functional senescence by increasing communication between networks to maintain cognitive performance. However, in our study, the networks were extracted based on their correlation patterns with a seed, and as such, increased RSFC does not reflect increased connectivity either within or between networks but rather with a seed. Given the different methodology between these studies and ours, it is difficult to draw strong conclusions. We do note, however, that aging does not affect RSFC in a simple way, regardless of the methodology employed.

The CRUNCH and HAROLD hypotheses suggest that older brains recruit additional regions as compensation to maintain performance during tasks (Reuter-Lorenz & Cappell, 2008; Cabeza, 2002). In older adults, the recruitment of additional resources leads to increased synchronization of neurons in regions that do not exhibit such coordinated activity in younger individuals, resulting in higher RSFC in these areas for older adults. It is possible that higher RSFC in older adults reflects compensation because of age-related neuroplasticity. Another interpretation is an age-related decrease in the ability to inhibit resting-state activity (Chen, Azeez, Chen, & Biswal, 2020). The origins of resting-state networks are the spontaneous fluctuations in brain activity that occur even in the absence of a task or stimulus. Resting-state networks are active when a person is at rest and inhibited when a person is involved in a specific task (Buckner, Andrews-Hanna, & Schacter, 2008). DMN activity is not only detected at rest but also during simple tasks (Greicius, Srivastava, Reiss, & Menon, 2004). It is therefore possible to consider the inhibition of spontaneous fluctuations as a fundamental ability of the brain to accomplish a task (Chen et al., 2020). According to this view, higher RSFC in older adults could reflect a decline in the ability to modulate resting-state activity to optimize functioning.

The Effect of Singing

The second specific objective was to identify potential RSFC differences between singers and nonsingers within the same five networks to shed new lights on the impact of singing on basic brain physiology. Our main hypothesis was that RSFC would be less affected by aging in singers compared with nonsingers, consistent with the notion that cognitively engaging activities such as singing can have a beneficial impact on brain aging (the Mental Exercise hypothesis). Our results revealed that group differences in RSFC were limited to the DMN. In the following paragraphs, we detail these differences, and then we discuss brain–behavior interactions.

The finding of stronger RSFC in the right SFG in singers is consistent with a longitudinal piano training study that was conducted with healthy young adults, which reported that RSFC in the right SFG in the sensorimotor network increased after 24 weeks of piano training, whereas there was no change in the auditory network (Li & Li, 2018). A cross-sectional study of RSFC in young musicians and nonmusicians also found that musicians had stronger RSFC in the right SFG (Luo et al., 2014). A longitudinal drumming course study conducted with healthy young adults reported that RSFC was higher in multiple regions including bilateral occipital gyrus and bilateral MTG after 8 weeks of drum training (Amad et al., 2017). A study on insula-based networks among professional classical musicians reported the RSFC between the insula and SFG was stronger in musicians than nonmusicians (Zamorano et al., 2017); however, Amad et al. (2017) reported that RSFC between the right STG and MTG was lower after drum training. Our results are also consistent with stroke rehabilitation studies in which 6 months of singing training increased RSFC in the bilateral STG and the left MTG. The stroke patients improved in verbal memory and language skills, and their RSFC was enhanced after 6 months of singing training in DMN (Sihvonen et al., 2020). However, further research examining the effects of singing on different brain networks is necessary.

In the present study, we found Age × Group interactions in RSFC in the DMN (bilateral precuneus), but not in the other networks. One reason may be that the DMN is typically more active during rest and reflect the brain spontaneous activities, which the differences in the DMN are easier to detect (Buckner et al., 2008). Another reason is that the "amateur" singing activities may not be sufficiently demanding to modulate the RSFC significantly in the other networks. In a previous study from our group, amateur singers were found to have a better articulatory accuracy in challenging situations compared with nonsingers (Tremblay, Gagnon, Roy, & Arseneault, 2023). However, in another study, we found that amateur singing had little effect on vowel articulation during reading (Marczyk, Belley et al., 2022) and speech-in-noise perception (Perron et al., 2021). Hence, the impact of amateur singing is not straightforward. It is therefore perhaps not surprising that its association with RSFC is only found in one, general network, the DMN.

The third specific objective of our study was to examine the relationship between RSFC and cognitive aging in singers and nonsingers to tackle mechanisms and implications. We hypothesized that stronger RSFC in singers would be associated with better auditory attention. To test this hypothesis, we investigated the association between auditory attention and the RSFC in the regions that showed age by group interactions in the DMN. We found that stronger RSFC in the DMN, more specifically in the bilateral precuneus, was associated with worse auditory attention. Previous studies have shown RSFC differences in the precuneus between professional musicians and nonmusicians (Zamorano et al., 2017; Tanaka & Kirino, 2016). Activity in the precuneus has been found to be associated with visuospatial imagery, episodic memory retrieval, self-processing operations (first-person perspective taking and an experience of agency), consciousness, and switching attention between different targets in space and between different object features (Cavanna & Trimble, 2006). During choir singing, following the choir director's instructions and reading music sheets involves sustained visual attention, which might explain the differences in the precuneus in singers. The TAiL is an auditory attention test rather than a visuospatial attention test. The higher RSFC in precuneus may have a negative effect on auditory–spatial attention tasks, which need further investigation in future studies.

The hypothesis that stronger RSFC is associated with better auditory attention was supported in young nonsingers in the bilateral precuneus in the DMN. In older singers and nonsingers, better cognitive performance was associated with lower RSFC (Ferreira & Busatto, 2013). Consistent with prior studies, our results suggest that the relationship between RSFC and cognitive performance is complex (for a review, see Ferreira & Busatto, 2013). Based on the CRUNCH and HAROLD models, older adults exhibit increased brain activity during tasks, which can be interpreted as "dedifferentiation" (Reuter-Lorenz &

Mikels, 2006; Cabeza, 2002). Dedifferentiation reflects reduced neural specialization in aging, resulting in increased functional similarity across diverse tasks (Cabeza, 2002). This functional similarity results in certain brain regions exhibiting increased RSFC, whereas others demonstrate decreased RSFC. From the inhibition perspective, tasks can disrupt RSFC, as the brain shifts its resources from a resting state to an engaged one. In this perspective, lower RSFC would facilitate the performance of complex cognitive tasks. The inhibition function of RSFC might decrease with age, and this may contribute to the decline in cognitive performance in older adults (Chen et al., 2020).

Limitations

In the present study, singing experience was heterogeneous across our sample of singers. Singers were engaged in various types of singing, the most frequent ones being classical, popular, and choir. Their range of singing experience was broad (from 2 to 62 years). Most singers never received formal training (73%). However, everyone had at least 1 year of experience, and sang every week for at least 60 consecutive minutes in an organized setup like a choir, a band, or a class. We did not investigate whether singing experience and singers' characteristics, such as music genres and singing styles, could affect RSFC to avoid overfitting the data, given our moderate sample size (41 singers). In a previous study, we reported that singing experience, such as age of onset, can affect cognition while training, and years of experience were not associated with cognitive performance (Tremblay & Perron, 2022). In that study, however, the sample size was larger (75 singers).

Future studies should strive to examine how different singing experiences can affect RSFC. For example, singers with more extensive singing experience may exhibit stronger RSFC within the auditory and motor networks compared with those with less singing experience. Long-term singing training may lead to increased RSFC within the memory network, as singers need to memorize lyrics, melodies, and other aspects of their repertoire. Singers who experience more global impacts on well-being and mental health could display stronger effect on general networks compared with those whose practice has fewer effects on well-being and mental health. In addition, our sample was well educated, with an average of 16.6 ± 3.04 years, which correspond to a bachelor's degree. Sixty participants (27 singers and 33 nonsingers) had a university degree. Higher education is related to higher cognitive performance and is known to offer some protection against cognitive decline in aging (Lövdén, Fratiglioni, Glymour, Lindenberger, & Tucker-Drob, 2020). Although both groups were matched in terms of education, their high education level may have reduced potential group differences in auditory attention, as well as in RSFC.

CONCLUSIONS

Our study of 84 healthy singers and nonsingers demonstrates that RSFC is not systematically lower with aging. Although RSFC was generally lower in older adults, some regions exhibited higher RSFC, suggesting compensatory mechanisms or a decline in inhibition of RSFC. The relationship between RSFC and cognitive performance was complex. RSFC in amateur singers differs from RSFC in nonsingers in the DMN, but not in the four other networks investigated: auditory, speech, language, and dorsal attention. Lower RSFC was mostly related to better auditory cognitive performance in the precuneus in the DMN for both singers and nonsingers. A possible explanation is that stronger inhibition of RSFC is associated with better cognitive performance, reflecting a regulatory mechanism. Although higher or lower RSFC cannot necessarily predict auditory attention in our study, we did find that RSFC was associated with auditory cognition attention (both distractibility and CR). Determining the extent to which singing can transform brain networks and contribute to successful aging is crucial to develop more inclusive theories of cognitive aging and because that singing is arguably the most universal, most popular, and most affordable musical activity. However, most studies focus on instrument playing rather than singing. The present study represents a first step toward this goal, but additional work is needed to further understand the effect of aging on functional connectivity (at rest, but also during tasks) in those engaged in singing and other musical activities and those not engaged in such activities. The comparison of different types of musical activities would help better understand whether different musical activities differently affect brain physiology in aging.

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Data Availability Statement

Individual data are not available because informed consent obtained from participants did not include consent to public data sharing and we were not granted the right to request it a posteriori by our local research ethics committee. The group maps, however, are available on Borealis, the Canadian Dataverse Repository (https://doi.org/10.5683/SP3/PSNGYT), as well as the aggregated behavioral data used in the brain–behavior analyses.

Author Contributions

Xiyue Zhang: Conceptualization; Data curation; Formal analysis; Methodology; Software; Visualization; Writing—Original draft. Pascale Tremblay: Conceptualization; Data curation; Funding acquisition; Investigation; Methodology; Project administration; Resources; Software; Supervision; Writing—Review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this paper report its proportions of citations by gender category to be: M/M = .417; W/M = .217; M/W = .133; W/W = .233.

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